ON THE RÔLE OF THE CAROTENOIDS IN PHOTOSYNTHESIS IN *RHODOSPIRILLUM RUBRUM*

by

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INTRODUCTION

In his well-known experiments on phototaxis of *Bacterium photometricum*, ENGELMANN[1-3] observed accumulation of this bacterium in various regions of a micro-spectrum projected on a culture in liquid medium. The location of these regions proved to correspond with the absorption bands of pigments present in the bacteria. In a series of experiments with diatoms and blue-green algae a similar relation was also found to occur between photosynthesis and absorption. ENGELMANN concluded from these observations that *Bacterium photometricum* would be able to photosynthesize.

BUDER[4] succeeded in demonstrating that in the blue-green part of the spectrum the bacteria collect in three separate bands (at 5300, 4900, and 4700 Å) instead of in one as was found by ENGELMANN.

From these data one might be inclined to conclude that carotenoids play a rôle in photosynthesis. FRENCH[5], however, after determining the action spectrum of photosynthesis in the purple bacterium *Spirillum rubrum*, suggested that carotenoids would not be involved in this process. The action spectrum was obtained by determining the amount of carbon dioxide absorbed per incident quantum at various wave-lengths. The absorption maxima of the carotenoids considered proved to be situated at 5500, 5100, and 4900 Å. Photosynthesis readings were done at 5780, 5460, and 4360 Å (mercury lines) and at 5000 Å (isolated by a double prism monochromator). The results suggested a continuous decrease of the rate of photosynthesis at decreasing wave-lengths in the said region of the spectrum. The data obtained by FRENCH are in agreement with the earlier results of GAFFRON[6] who determined the rate of photosynthesis in *Thiocystis* in three regions of the spectrum (7200–9000, 6200–6900, and 4200–4500 Å). However, we must observe that a reliable action spectrum can hardly be derived from the few scattered observations made by these investigators.

After quoting the experiments of BLAAUW[7], CASTLE[8], JOHNSTON[9], and VOERKEL[10], which prove blue light to be effective in both phototropism and phototaxis, FRENCH[5] remarks that it would be "reasonable to expect that in the spectrum projection experi-

* This investigation has been made possible by a grant from the Rockefeller Foundation and from the "Stichting voor Zuiver Wetenschappelijk Onderzoek i.o."

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ments purple bacteria would collect only at the bands of the carotenoids". However, the bacteria did collect in the infra-red and at the 5900 Å band as well. This phenomenon is supposed to be due to a chemotaxis "in a carbon dioxide gradient caused by carbon dioxide utilization in light which is most active for assimilation". So FRENCH suggested that two separate mechanisms underlie phototaxis, each acting in different regions of the spectrum. Since, moreover, an action spectrum for photosynthesis was obtained in which only bands occurred corresponding with the absorption bands of the green pigment, it was concluded that in the bacteria in question the carotenoids play no rôle in photosynthesis.

Several authors succeeded in demonstrating a relation between carotenoids and photosynthesis in other organisms. Among them we cite MOTHES, BAATZ, AND SAGROMSKY[11] (experimenting with the diatoms *Biddulphia sinensis, Coscinodiscus excentricus*, and *Chaetoceras simplicia centrosperma*), DUTTON AND MANNING[12] (with a diatom, *Nitzschia closterium*), EMERSON AND LEWIS[13] (with the blue-green alga *Chroöcoccus*), EMERSON AND LEWIS[14] (with the green alga *Chlorella*), and WASSINK AND KERSTEN[15] (with the diatoms *Nitzschia dissipata* and *Nitzschia spec.* cf. *ovalis*).

MANTEN[16,17] determined the action spectrum of phototaxis by means of the bacteriophotometer according to MILATZ AND MANTEN[18]. This apparatus enables the establishment of two light fields with a distinct boundary on a slide under the microscope. By keeping constant both the wave-length and the intensity of the light in one field (field of comparison) and by irradiating the other field with light of any desired wave-length, the intensity of which can be varied, one is able to estimate the phototactic activity of this light as compared with that of the constant light by adjusting its intensity until the bacteria are no longer able to perceive the boundary (do not show any shock reactions when passing it). In this way a fairly accurate relative action spectrum of phototaxis can be obtained.

By comparing this action spectrum with the absorption spectra of the bacteria, of an aqueous extract as well as of the isolated pigments, MANTEN concluded that both the bacterio-chlorophyll and one or two carotenoids are active in phototaxis. The identity of the active carotenoids could not be established with certainty; it seemed reasonable, however, to assume that rhodopin as well as rhodopurpurin are active in phototaxis. Remarkably, the most abundantly occurring carotenoid, spirilloxanthin (= rhodoviolascein) proved not to be involved in this process.

Furthermore, in agreement with SCHRAMMECK[19], MANTEN demonstrated that the contrast sensitivity—defined as the ratio of the intensities of two light fields at equal wave-length for which the bacteria, crossing the boundary, just show a shock reaction—which is constant at lower light intensities, decreases rather abruptly beyond a certain light intensity. This limit is generally characteristic of light saturation in photosynthesis (*cf.* WASSINK, KATZ AND DORRESTEIN[21]). From these data MANTEN concluded: ". . . that phototactic reactions of purple bacteria are induced by a sudden decrease in the rate of photosynthesis", moreover he suggested that, because of this relation: ". . . the action spectrum of phototaxis in *Rhodospirillum rubrum* may be considered to be the same as the action spectrum of photosynthesis". Possibly the participation of the carotenoids in photosynthesis might be too small to exceed the limits of error of the technique used by FRENCH.

It seemed of interest to test the above-mentioned hypothesis by direct determination of the action spectrum of photosynthesis in *Rhodospirillum rubrum*, which is the

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object of the present paper. With regard to the foregoing we restrict ourselves to the spectral region in which absorption of the carotenoids occurs. Accordingly, the infra-red part of the spectrum has been neglected in this study.

METHODS

Rhodospirillum rubrum Esmarck strain 4, the same one as used by MANTEN, and originally isolated by VAN NIEL[21], was grown in a solution of 1% peptone POULENC and 0.5% sodium chloride in tap water. This medium was the same as that used by MANTEN in his experiments. Culture conditions (light cabinet, temperature varying between 25 and 32°C) also were the same as those applied by this author.

Photosynthesis was determined with the WARBURG technique. In the above-mentioned culture medium, however, the bacteria did not show any appreciable gas exchange. So it was necessary to suspend the bacteria in a medium which leads to a distinct carbon dioxide uptake in light. We used 0.015 *M* sodium butyrate in 0.01 *M* phosphate buffer p_H 7.2 as indicated by GAFFRON[22],

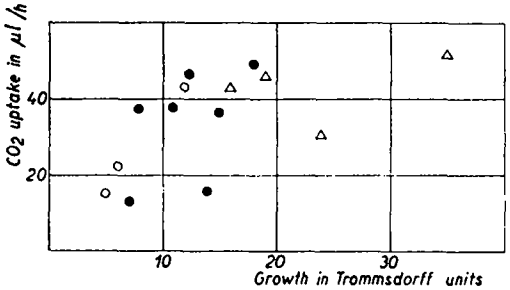

Fig. 1. Demonstration of bad correlation between the rates of growth and photosynthesis at light saturation. Age of the cultures: o: 1 day, •: 2 days, △: 3 days

Photosynthesis in *Rhodospirillum rubrum* is rather sensitive to culture conditions and treatment. This was shown by the divergency in rate of this process at light saturation in the various cultures, even if the cultures appeared to be quite identical in colour and in density. Often good development did not coincide with a high rate of photosynthesis at light saturation (*cf.* Fig. 1). As a result of preliminary experiments the following procedure was adopted which enabled us to obtain satisfactory material. The bacteria were cultivated in 100 ml glass-stoppered bottles, containing the peptone medium mentioned. Every three days a new inoculum was made by transferring 1 ml of such a culture into fresh medium. Before filling the bottles the sterile medium was boiled during 5 minutes in order to expel all oxygen. The medium was allowed to cool down to 25°C in the bottles before inoculation. Subculturing proved to stimulate the photosynthetic activity. After treating the bacteria in the described manner for some weeks the maximal rate of photosynthesis often decreased spontaneously (sometimes down to 25% of the maximal value). After prolonged subculturing of such a series this rate proved to increase again after a few weeks. The change in activity occurred within two or three days. The cause of these phenomena was not studied so far.

In order to avoid these complications we started a second subculturing series by transferring the bacteria to fresh medium only once monthly. From this "one month"-series a new "three days"-series was grown if the photosynthetic activity of the running one was found to decrease. So far two successive inoculations proved sufficient.

The bacteria were prepared for experimental use as follows. 100 ml of the culture were filtered rapidly through filtering paper in order to assure homogeneity of the bacterial suspension. Next this suspension was centrifuged at an acceleration of about 1.3×10^6 cm/sec^2 during 15 minutes. The supernatant fluid was decanted and the

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bacteria were resuspended in 50 ml of the buffered butyrate medium solution mentioned above. After centrifuging again for 15 minutes the solution was decanted and the organisms were again suspended in fresh butyrate medium up to a concentration of 20 Trommsdorff units per ml. Repeated washing proved to be harmful.

In order to establish anaerobic conditions a gas mixture of N_2/5% CO_2 (freed from the last traces of oxygen by passing it through a reduction oven) was led through the suspension. After 15 minutes 2 ml were pipetted into each WARBURG vessel (bottom area about 7 cm^2). Finally, the gas mixture was passed through the manometers with vessels attached during 15 minutes.

The bacteria were accommodated in the thermostat at 35.5°C during at least 45 minutes in the light. Apart from two thermo-barometers the definite experiments were run with four vessels: a dark control (painted black), a second flask in which the spirilla were kept at light saturation (sodium light) throughout the experiment in order to check the constancy of the optimal photosynthetic rate, the third and the fourth ones were respectively illuminated with sodium light and with light of the wave-length to be tested. In the latter two vessels the light intensity could be varied by placing neutral glass filters (Schott NG5 and NG8 in various combinations) against the bottom.

Light was introduced into the thermostat through a glass plate in the bottom which was coated with black paper, except for three windows. Each of these permitted the illumination of the bottom of a single WARBURG vessel. By means of lenses the incident light was made nearly parallel. Over the sodium lamps an infra-red filter (1 cm layer of 6% $CuSO_4$ solution) was adjusted. Light of variable wave-length was obtained by means of a CHRISTIANSEN-WEIGERT[23] filter (dispersion monochromator). For the longer wave-lengths down to 5200 Å a 12 V 100 W projection bulb (Philips E27) was used as light source. When shorter wave-lengths were required this lamp was replaced by a high power projection bulb (30 V 900 Watt, Philips E40). In this case we used an infra-red filter as mentioned above.

The composition of the light (energy distribution in the spectrum)—dependent on the temperature of the filter thermostat—was determined by means of a VAN CITTERT[24] monochromator with photocell and a.c. amplifier according to MILATZ[25, 26]. To this purpose the light transmitted by the filter was focussed on the slit of the double monochromator. The energy calibration was carried out by using a calibrated band lamp. The half value of the triangular regions transmitted by the double monochromator amounted to about 20 Å. Though this value is rather small it was taken into account in the correction. Incident light intensity (total energy) measurements were carried out with a standardized thermopile.

Principle of the determination of the action spectrum of photosynthesis

It is mentioned in literature that in weak light photosynthesis of various *Thiorhodaceae* and *Athiorhodaceae* is not linearly proportional to the incident light intensity. The curve of photosynthesis *versus* incident intensity is stated to show a sigmoid shape in this intensity range. WASSINK *et al.* presumed this phenomenon to be due to a competition of internal and externally supplied hydrogen donors.

However, from a large number of preliminary experiments it appeared that rather considerable deviations from this type of curve occur in *Rhodospirillum rubrum*. A more detailed study of this problem is in progress now. Moreover, as has already been mentioned, the rate of photosynthesis at light saturation showed marked variations for

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bacteria obtained from different cultures. In view of this the following comparative procedure was adopted. The activity of a given wave-length of light was compared with that of a fixed wave-length with material of the same culture. For the wave-length of comparison sodium light was used throughout. This was done as follows.

In each experiment photosynthesis was determined for both wave-lengths at three light intensities in a region in which the rate of photosynthesis shows a nearly linear dependency on light intensity. If the rate of photosynthesis is plotted against incident intensity, intensities of both kinds of light yielding the same standard rate of carbon dioxide uptake (5 or 10 μl CO_2/hour) could be established. Their quotient expresses the relative activity of the examined wave-length (*cf.* Fig. 2).

The correctness of this method depends on the constancy of the mentioned quotient over the whole range of both curves. This means that in one culture the type of the light-assimilation relation must be equal for light of any wave-length. The results showed that these conditions were satisfactorily fulfilled.

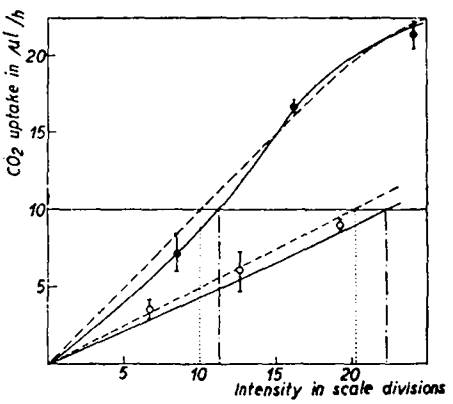

Fig. 2. Example of the determination of W_λ for λ=5700 Å. •: sodium light. o: light of 5700 Å. This example was chosen since it is doubtful here whether the ascending part of the light/photosynthesis curve is straight or sigmoid. In drawing each set of curves care was taken that the quotients of the distances to the ordinate of points of both graphs situated at equal distance from the abcissa would remain the same. In this way it proved possible to plot two sets only. W_λ computed from drawn lines: 0.50; from dotted lines: 0.52. The mean value, 0.51 $\pm$ 0.01, was plotted in the action spectrum (Fig. 5)

Preliminary experiments

In order to establish the optimal conditions for photosynthesis of the strain used some introductory experiments were performed.

Influence of temperature. Fig. 3 shows the saturation rate of photosynthesis at different temperatures. Seven vessels were run simultaneously. In the graph the mean values obtained are plotted. At each temperature three 10-minutes readings were made. During the experiment the temperature was raised successively. The bacteria were allowed to accommodate at each temperature during 15 minutes. In consequence of these data we decided to perform the following experiments at 35.5° C.

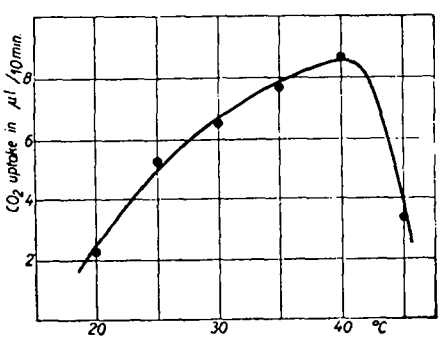

Fig. 3. Influence of temperature on rate of photosynthesis at light saturation

Influence of p_H. The rate of photosynthesis in *Rhodospirillum* proved to be highly dependent on p_H (*cf.* Fig. 4). In all experiments 0.01 m phosphate buffers were used. Since the optimum is rather sharp it seemed advisable to maintain a nearly optimal p_H (7.2) in our definite experiments. The determinations were done *in triplo.*

Influence of age of culture. From a stock suspension several flasks were inoculated. Every day a culture was tested. Optimal photosynthesis proved to occur in 4–6 days old

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cultures. However, in order to assure constant assimilation rates as far as possible 3 days old suspensions were used as a rule.

Substrates. Apart from sodium salts of formic, acetic and butyric acid, isopropanol was also tested as a substrate. According to FOSTER[27] an unidentified photosynthetic non-sulfur purple bacterium was capable of using the latter substance in the light by converting it quantitatively into acetone coupled with carbon dioxide reduction. *Rhodospirillum rubrum* was found to be able to use this compound too. The rate of carbon dioxide uptake, however, turned out to be much slower than it was with fatty acids; the rate of gas uptake with sodium butyrate was about five times as high. As mentioned above, the latter substrate was used in our definite experiments.

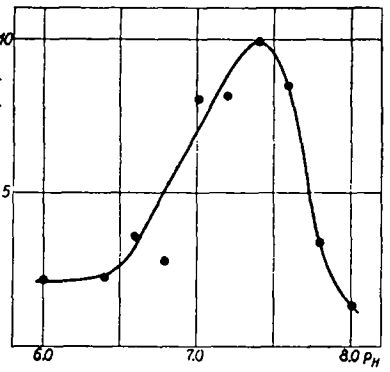

Fig. 4. Influence of p_H on rate of photosynthesis at light saturation

In addition the ratio: moles carbon dioxide consumed/moles butyrate converted was determined. The mean value of the results of nine experiments amounted to 1.40. Exactly the same figure (from nine determinations) was found by GAFFRON[22] when studying the photosynthetic metabolism of an *Athiorhodacea* closely resembling *Rhodovibrio* or *Rhodobacillus*.

The action spectrum. Based on the data contained in Table I (the photosynthesis figures are the average of three 15-minutes readings) the relative effectiveness of the variable wave-lengths, determined as described above, yielded the relative action spectrum shown in Fig. 5. The ordinate represents the ratio between the effectiveness of

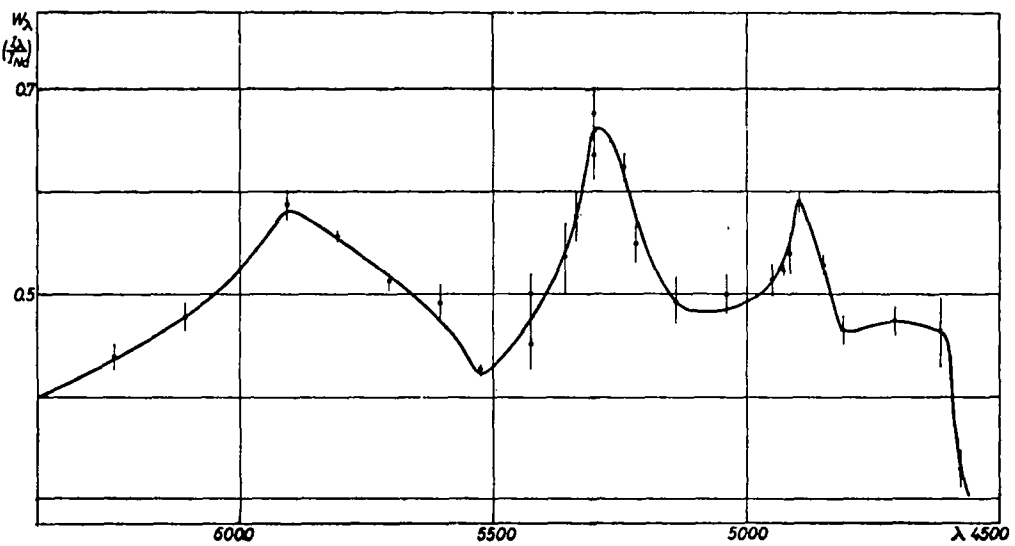

Fig. 5. Action spectrum of photosynthesis. Values computed as described in text of Fig. 2

I_λ and I_{sodium}, I being expressed in thermopile-readings. The abcissa shows the wave-lengths in Å. No corrections were made for characteristics of the apparatus, nor for

TABLE I

EFFECTIVENESS OF SODIUM LIGHT AND OF DIFFERENT WAVELENGTHS IN PHOTOSYNTHESIS OF *RHODOSPIRILLUM RUBRUM*

Exp. no.	Photosynthesis in sodium light in μl/h	I_{Na} in arbitrary units	λ in Å	Photosynthesis in light of wave-length λ in μl/h	I_λ in arbitrary units
4	10.0 25.2 52.8	6.3 9.9 66.4	6420	4.6 5.6 13.2	8.4 13.1 19.6
5	10.6 12.8 16.0	7.8 12.6 18.9	6240	4.2 4.8 11.6	7.6 13.7 20.0
6	8.0 18.0 57.6	8.2 13.0 64.6	6100	3.7 6.0 10.0	7.2 13.5 19.5
7	11.2 16.4 48.0	8.0 15.8 62.7	5900	5.0 6.8 14.4	6.6 12.7 18.5
8	15.2 23.2 52.6	12.5 24.2 65.5	5800	— 2.0 8.8	— 7.8 14.4
9	7.2 16.8 41.3	8.3 16.3 66.1	5700	3.7 6.0 8.8	6.8 12.6 19.1
10	4.8 14.4 23.5	7.8 11.9 64.6	5600	3.2 3.2 7.2	5.7 10.5 15.1
11	11.2 20.4 24.8	7.2 14.8 22.6	5520	2.4 4.8 6.0	4.4 8.2 11.8
12	6.4 8.8 50.4	8.1 12.2 63.4	5420	1.6 2.0 4.0	2.9 6.0 9.6
13	10.1 20.4 60.4	6.5 15.0 63.4	5420	2.4 4.0 6.0	4.6 6.9 12.3
14	9.6 12.0 18.4	7.4 15.3 65.0	5350	6.4 4.8 5.2	4.8 7.0 12.3
17	8.0 13.6 35.2	8.0 12.9 70.7	5330	1.3 4.0 —	6.4 9.6 —
18	8.0 11.2 18.8	8.7 18.2 25.9	5300	2.4* 0.0 7.2	4.9 9.5 14.1
20	10.4 16.4 15.2 32.8	8.3 16.0 24.4 70.7	5210	6.9 8.0 — 12.4	10.0 15.6 — 28.2

TABLE I (continued)

Exp. no.	Photosynthesis in sodium light in μl/h	I_{Na} in arbitrary units	λ in Å	Photosynthesis in light of wave-length λ in μl/h	I_λ in arbitrary units
21	8,0 11.2 14.8 26.0	13.9 20.4 70.5	5130	7.6 9.6 —	22.0 32.5 —
22	12.8 17.2 40.4	13.5 19.9 67.8	5030	9.2 12.8 —	18.2 26·9 —
23	14.8 18.0 41.6	15.5 26.1 67.8	4940	5.2 8.0 —	10.5 19.9 —
24	11.2 16.4 52.8	8.8 12.9 69.0	4920	3.7 5.2 12.0	7.2 10.2 18.8
25	5.6 12.4 17.2	8.0 12.6 68.5	4910	1.1 3.2 5.6	6.0 11.8 18.5
27	9.6 21.2 45.6	7·5 22.3 67.6	4800	2.8 4.4 5.0	4.8 9.0 13.6
30	4.8 11.2 15.6	7.4 11.9 68.4	4700	2.4 2.0 8.4	6.5 12.3 18.1
31	11.6 14.4 45.2	7.6 11.7 67.9	4610	4.0 4.8 —	5.1 7.9 —
32	7.2 11.2 10.4	7·3 12.1 18.7	5300	9.6 17.2 26.8	26.6 39.0 67.9
33	8.0 9.6 42.5	8.4 12.1 67.0	5300	6.1 6.8 —	8.8 16.3 —
34	4.8 8.0 8.8	8.0 12.1 23.7	5230	5.1 4.8 7.2	7.0 12.6 18.1
35	7.4 9.2 10.4	8.0 12.1 23.6	4890	3.7 5.2 7.2	6.1 10.9 16.3
36	8.5 14.8 27.6	7.9 12.2 22.8	4800	5.1 10.0 14.0	11.2 19.3 28.9
38	5.8 9.6 23.2	7.1 13.5 21.9	4840	5.1 8.0 15.6	12.4 23.1 35.0
39	10.1 14.4 19.2	7.4 11.8 17.6	4570	2.9 6.0 8.0	7.4 13.5 20.8

* Single reading.

diffraction and absorption by the cell suspensions. Since these factors lead to some deformation the action spectrum given only has an approximate character.

It will be noted that definite maxima occur at 5900, 5250, 4900, and 4600 Å.

DISCUSSION

If one compares the action spectrum of photosynthesis with the absorption spectra of the colloidal extract as well as that of a suspension of living cells according to MANTEN[17, 18] it becomes evident that the 5900 Å peak corresponds to a bacteriochlorophyll absorption maximum, whilst the maxima at 5250, 4900, and 4600 Å must evidently be ascribed to the activity of carotenoids. So it is proved that carotenoids play a rôle in the photosynthesis of *Rhodospirillum rubrum*.

Both absorption spectra, published by MANTEN, show a maximum at 5500 Å. In the action spectrum of photosynthesis, however, instead of this maximum a minimum occurs. So we must conclude that not all carotenoids are involved in the absorption of photosynthetically active light. From the comparison of the action spectrum of photosynthesis with the absorption spectra of the carotenoids, isolated by MANTEN, it should be concluded that the main carotenoid, spirilloxanthin, is inactive in photosynthesis.

The fact that the location of the maxima and minima in both spectra turns out to be exactly the same is strongly in favour of MANTEN's hypothesis concerning the identity of the action spectra of phototaxis and of photosynthesis in these bacteria. It also gives strong support to MANTEN's hypothesis that the phototactic reactions are based on the photosynthetic process, and that, accordingly, the same pigments are involved in both phototaxis and photosynthesis.

As mentioned above, the action spectrum for photosynthesis presented in Fig. 5 is somewhat deformed, since the half width values of the regions transmitted by the CHRISTIANSEN filter are rather significant, especially at the longer wave-lengths (up to 300 Å). This can easily be seen from the graph; at 5900 Å W_λ must amount to 1.0, since in this case the light transmitted by the dispersion monochromator ought to be of the same wave-length as that of sodium light (light of comparison). In fact W_λ amounts to about 0.6. This deviation will be due to the accompanying less active wave-lengths, which also pass the filter. On the other hand it should be kept in mind that their energy is also registered by the thermopile.

Moreover, no corrections have been made for diffraction and absorption of the light by the cell suspensions. So it is clear that the action spectra of phototaxis and of photosynthesis cannot be compared in an absolute way.

An attempt was made, however, to correct both spectra in such a manner that quantitative conclusions might be drawn. In this respect my thanks are due to Mr L. N. M. DUYSENS for his valuable theoretical help and to Mr A. J. TH. MAASSEN for carrying out the determinations.

By means of an optical integrator according to BURGER and VAN CITTERT[28], MANTEN's phototaxis action spectrum was first corrected for infinitely small regions transmitted by the double monochromator used by this author. Next, with the aid of the integrator, the corrected spectrum thus obtained was submitted to a deformation which would have resulted if MANTEN had also made use of the CHRISTIANSEN filter. In this way a graph (Fig. 6a) was obtained representing the phototaxis spectrum as determined with light of the same composition as used in the photosynthesis experiments

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The slit widths used by MANTEN were not known exactly, so they had to be estimated. For this reason we present this graph with some reserve; deviations, however, will be of minor importance.

Since MANTEN used a single cell method, absorption could be neglected in his experiments. In our bacterial suspensions, however, absorption fluctuated between 40 and 65 %. So the photosynthesis action spectrum was also corrected in this respect (Fig. 6b).

In Fig. 6 both graphs obtained are plotted in such a way that the maxima at 5900 Å, due to bacteriochlorophyll, nearly coincide. It is evident that the maxima due to carotenoid activity are much more pronounced in the photosynthesis action spectrum than they are in the action spectrum of phototaxis. Moreover, the photosynthesis spectrum as a whole is situated on a higher level than the phototaxis spectrum in the region in which the carotenoids are absorbing. Apparently the activity of the carotenoids is much more pronounced in photosynthesis than it is in phototaxis. The following explanation of this phenomenon is suggested here.

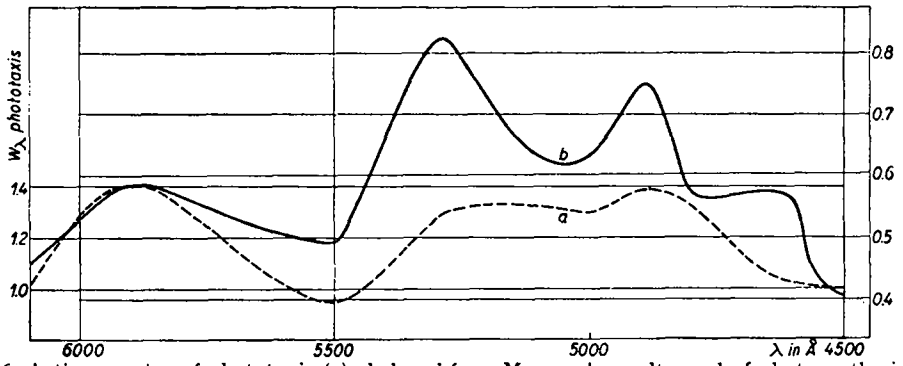

Fig. 6. Action spectra of phototaxis (a), deduced from MANTEN's results, and of photosynthesis (b). Explanation see text.

According to EMERSON AND LEWIS[15] respiration in *Chlorella* is stimulated in light absorbed by the carotenoids. If we assume an analogous phenomenon to occur in *Rhodospirillum rubrum* we might explain the discrepancy between the carotenoid activity in phototaxis and in photosynthesis as follows. According to MANTEN's hypothesis phototaxis is based on photosynthetic processes. Now we must realize that evidently the products of photosynthesis are used in different processes, *viz.* formation of cell constituents, and of dissimilation products yielding the energy needed by the cell for different purposes, amongst other for phototaxis. If one of these processes is stimulated one or more of the other processes may be retarded, since less of the assimilation product will become available for them. In this way it seems plausible to assume that the stimulation of phototaxis by carotenoids in *Rhodospirillum rubrum* is not as large as may be expected from the photosynthetic activity of these pigments. Since, however, also judging from the results of dark experiments, no gaseous dissimilatory products will have been formed, under the conditions of our experiments this working hypothesis could not be checked directly.

SUMMARY

The photosynthetic action spectrum of *Rhodospirillum rubrum* Esmarck strain 4 was determined. Some carotenoids were found capable of absorbing photosynthetically active light. Apparently, however, the main carotenoid, spirilloxanthin, does not participate in photosynthesis.

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Maxima and minima of the action spectra of photosynthesis and of phototaxis were found to coincide. Thus the correctness of MANTEN's[16, 17] hypothesis concerning a direct connection between both processes is strongly supported.

The carotenoid action seemed to be less pronounced in phototaxis than it is in photosynthesis. In the discussion a hypothetical explanation of this phenomenon has been given.

RÉSUMÉ

Le spectre de l'action photosynthétique de *Rhodospirillum rubrum* Esmarck No. 4 a été déterminé.

Quelques carotinoides paraissent capables d'absorber de la lumière active pour la photosynthèse. Le pigment principal, cependant, la spirilloxanthine, ne semble pas prendre part à ce processus.

Nous avons constaté que les maxima et les minima des spectres de l'action de la photosynthèse et de la phototaxe coïncident. C'est là un argument important en faveur de l'hypothèse de MANTEN[16, 17] concernant la relation directe entre les deux processus.

L'action des carotinoides nous a semblé moins prononcée dans la phototaxe que dans la photosynthèse.

Nous présentons dans la discussion une explication hypothétique de ce phénomène.

ZUSAMMENFASSUNG

Das Wirkungsspektrum der Photosynthese von *Rhodospirillum rubrum* Esmarck Stamm 4 wurde festgestellt.

Es stellte sich heraus, dass einige Carotinoide imstande sind photosynthetisch actives Licht zu absorbieren.

Es ist aber sehr wahrscheinlich, dass das hauptsächlich vorkommende Carotinoid, Spirilloxanthin, nicht an der Photosynthese teilnimmt.

Zusammenfallen der Maxima und Minima der Wirkungsspektra der Photosynthese und der Phototaxis ist eine wichtige Stütze für MANTEN's[16, 17] Hypothese einer direkten Korrelation dieser beiden Prozesse. Die Aktivität der Carotinoide ist wahrscheinlich geringer in der Photosynthese als in der Phototaxis. Eine Hypothese zur Erklärung dieser Tatsache wird in der Diskussion besprochen.

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Received November 1st, 1949